A NEW THEORY OF THE MECHANICAL EVOLUTION OF THE METAPODIAL KEELS OF DIPLARTHRA.

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In the last number of the Journal of Morphology, Mr. Austin Carey gives the results of his studies in the foot structure of the Ungulates. A fair statement of his main conclusions, or rather perhaps the pith and substance of his argument is to be found in the concluding sentence of his article which reads as follows: "That the lines of evolution have progressed with but few useless side variations seems to be the uniform testimony of paleontologists; but that race changes follow those produced in individual life, or that they are directly caused by their mechanical surroundings, I do not think has been satisfactorily shown."

It is not my intention to enter here into a criticism or general discussion of the points this author has raised in his argument, nor will I undertake to discuss at this time the broad question of the transmission of acquired characters. I do, however, wish to say a few words upon the question of the production of crests and keels upon the distal extremities of the metapodial bones. Upon this point Mr. Carey says, (p. 341) "The crests and grooves on the lower metacarpal ends in some forms, produced apparently in relation to the sesamoid bones, is one of the most marked examples of probable mechanical evolution." "But before such structures can be said to prove the inheritance of acquired characters, the question should be tested whether they are not produced somewhere in the history of each individual by the necessary interaction of parts." He further adds in a footnote that "The crests in certain highly specialized forms, like the horse and deer, reach round to the anterior face of the bone and apparently cannot thus be interpreted or assigned to any mechanical origin that is obvious."

With reference to Mr. Carey's first proposition that these metapodial crests are produced during the life of each individual by the necessary interaction of parts, it appears to me to be a very simple one indeed. If they are produced, by pressure during the lifetime of each individual, and are not inherited, then clearly we should find the crests absent in new born animals that had never walked, and in which the metapodials had not been subjected to any impact or pressure whatever. I have taken the trouble to examine a number of such examples in which the distal ends of the bones were entirely cartilaginous, and I find that the keels and grooves are as well developed as they are in the adult animal. I will cite one case in particular in which I happen to know the history completely. During the past winter, a young hippotamus was born in the Zoological Gardens in Central Park, and it was stated to have been a premature birth; the animal lived but twenty-four hours, and I was informed by the keeper that it never stood upon its feet. An examination of the feet shows that the distal ends of the metapodials are entirely cartilaginous, and in them the keels are as well prefigured in cartilage as they are performed in bone in the adult animal. I have also found the same to be true of newborn rabbits and guinea-pigs. In another case of a young buffalo calf preserved in the American Museum Collection, the distal keels of the metapodials are complete notwithstanding the fact that the epiphyses of all the bones are very imperfectly ossified. This evidence, it appears to me, effectually disposes of the question of the production of these structures during the lifetime of the individual. They are as truly inherited as is the number of digits or any other important organ in the animal economy.

Mr. Carey further states in his concluding remarks that "Plasticity of bone, using the word *plasticity* not in a physical sense merely, but to include absorption under pressure, will probably account for much structure in the foot and elsewhere, especially in connection with the joints and in the field of variation and correlation." Now just what Mr. Carey means by "absorption under pressure" is not clear to my mind. If he means a process similar to that of the absorption of the roots

of the temporary or milk teeth, then the term " under pressure " is especially inappropriate, since Tomes has shown[1] that this process is entirely independent of pressure of any kind whatever, but is in some way connected with the presence of " myeloid " or " giant " cells. The only other process of " absorption under pressure " with which I am acquainted, is a pathological one. In this case the pressure is sufficiently severe to cut off entirely, or seriously affect the supply of nutrition, thereby causing the death of the part and its subsequent removal by sloughing. This however may be very gradual, so gradual in fact, as to resemble a perfectly normal change, as is often seen in the pressure of an aneurismal sac upon a neigboring bone. It may be true that a process of this nature, having its origin in a strictly pathological cause, may have become normal. Indeed, Huxley has remarked[2] that it is not always easy to draw the line between pathological and normal changes. Upon the whole, however, it seems to me that before we can admit this principle of "absorption under pressure" as having played any important part in the modification of the skeleton, we must require further proof of its existence and its method of operation.

That living bone tissue is plastic, I should say *highly* plastic and that too in the ordinary physical sense, is so abundantly demonstrated upon every hand, that no further argument is necessary to establish the truth of this proposition. It is recognized and acted upon in everyday surgical practice, and the number of cases wherein entirely new joints have been formed in old dislocations, leaves nothing to be desired to complete the proof. The changes thus produced however, have all occurred within the lifetime of the individual and it yet remains to be proven that they are capable of transmission to succeeding generations.

With reference to the production of the metapodial keels or crests, Cope has explained it in the didactyle foot at follows[3] : " A similar cause produces a similar result in the development

[1]Dental Anatomy, p. 197.

[2]Address to the British Medical Association, London Lancet.

[3]The Artiodactyla, American Naturalist, March 1889, p. 115.

of the tongue and groove articulation between the metapodials and first phalanges. In alighting on a didactyle foot, the toes are naturally spread, the result being to throw both the first phalanges away from the median line, or axis of impact, in divergent directions. The result of this impact is to produce upon each metapodial condyle as in the case of the humerus, an external roller of smaller diameter than the rest of the condyle, and separated from it by an abrupt crest. In both humerus and metapodial bones these crests are accentuated by a pinching process during flexion and extension. This is produced by the longitudinal torsion which results in all limbs in motion from the arrest of the outward rotation of the foot by the earth on alighting. The pinching of a keel by its groove takes place at all points in the length of the former, reached by the opposite sides of the extremities of the latter during flexion and extension. This keel becomes acute and prominent in the Boöidea and extends to the anterior face of the condyle. This development has been apparently especially due to the presence of two sesamoid bones, embedded in the flexor tendons, one on each side of the middle line of the posterior side of the metapodial condyle. The fissure between these two bones has permitted the moulding of the surface into a keel to fit it. That this has been the case is further indicated by the fact that a median trochlear surface exists at the distal extremity of the first phalanx in all mammals. But a single flexor tendon crosses this articulation, and it contains but one sesamoid bone, to which the trochlear surface is moulded in a concave surface, as is the case of the patella and the rotular groove of the femur."

In support of Cope's proposition, that the development of crests or keels upon the plantar or palmar aspect of the distal end of the metapodials, is due primarily to the presence of two sesamoids imbedded in the flexor tendons, I can add that in every case where these sesamoids are present, and pressure is exerted by the flexure of the phalanges upon the metapodials, the keels are developed, and conversely, that where the sesamoids are absent or are present without pressure, the keels are absent. The human foot and hand are

excellent examples of this. In the foot there are two sesamoids developed in the tendons of the *flexor brevis hallucis* as they pass over the end of the metatarsal of the great toe, to be attached to the phalanx. Now in the act of walking the greater part of the weight of the body falls upon this digit and as the heel is raised and the foot is brought into a more or less vertical position, these tendons are put upon the stretch and pressure results; in this metapodial, therefore, we find the keel present. In the other digits the sesamoids are absent and there is no keel developed. In the upper extremity there are sesamoids developed in the tendons of the *flexor brevis pollicis* at the metacarpo-phalangeal articulation, but owing to lack of pressure the keel is absent. Again in the Spider Monkey there are two sesamoids present in the tendons of the short flexors of the great toe and the keel is developed, while in the other digits there are no sesamoids and no keels. In other species of monkeys on the other hand such as the Macaques, the sesamoids are present and the keels are developed upon all the metapodials. These monkeys are said to be less arboreal in their habits, which would explain the difference in the matter of sesamoids and keels. Among the Marsupials there is no patella in the Vulpine Phalanger, and here we find that the rotular groove of the femur is very little developed. The hallux is without the sesamoids and there is no keel, notwithstanding the fact that there are both sesamoids and keels in the other metapodials. These cases could be multiplied indefinitely showing the same results. I have in fact failed to find a *single example of a metapodial*, in which sesamoids are present and pressure is exerted, *which does not show the presence of the primary keel.*

I will now consider Mr. Carey's other proposition viz: that the crests or keels in certain highly specialized forms reach around to the anterior face of the bone, and are not explainable by, nor cannot be assigned to any mechanical reason that is obvious. I must say that when I met with this problem several years ago, I was somewhat at a loss to understand how any mechanical explanation could possibly be applied to its Professor Cope's explanation of the extension of these keels in

the didactyle foot may possibly be the correct one, but I am inclined to doubt it seriously. It certainly cannot apply to the monodactyle foot since it is inconceivable that any "pinching" could occur in flexion and extension of the phalanges upon the metapodials; for the reason that there is no spreading such as he describes in the didactyle foot. It is moreover manifestly impossible that the sesamoids could have come into play to form the keel, because the amount of extension necessary to bring them into the proper position would be so great as to cause complete dislocation of the phalanx. How then can this extension of the keels be explained upon the basis of mechanics?

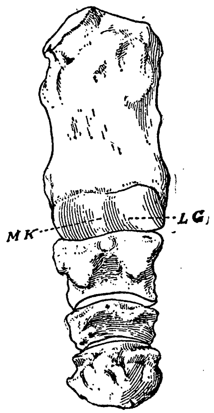

FIGURE 1.—*Coryphodon*, Median digit of the Manus, posterior view. (Coll. Am. Mus. Nat. Hist.)

In the first place it is necessary to call attention to the fact that at least three positions have been assumed in the various stages of the evolution of the ungulate foot, viz: a plantigrade or subplantigrade position, in which not only the phalanges but the metapodials are applied to the ground in walking, as in the hind feet of *Coryphodon* and all the earlier forms; second, a digitigrade position, in which only the phalanges are applied to the ground in walking, as in such forms as the tapir, rhinoceros and the earlier representatives of the horse series; and finally the unguligrade position in which the weight of the body is supported entirely upon the terminal or ungual phalanges. This position of the foot

belongs to the higher forms of both the odd and the even-toed ungulates. Now if we attempt to trace the history of the metapodial keels in the evolution of such a form as the horse, no one will deny, it seems to me, that we have here an unusually complete phylum represented, which clearly indicates the different stages in their development. In the earlier members of this series, such for example as *Hyracotherium*, the keels are confined to the plantar and palmar surfaces of the metapodials, and the animal was subdigitigrade. In such a form as *Mesohippus*, on the other hand, we pass from the digitigrade position of the foot to that of the unguligrade, wherein the weight of the body was supported upon the terminal phalanx or coffin bone. Just what induced this change is unknown, but it is more than probable that it was in some way connected with the reduction of the lateral toes.

We do not yet know with certainty the ancestors of the horse series beyond *Hyracotherium*; but there can be little doubt that the feet were pentadactyle and plantigrade. So far at least as the metapodials are concerned, we have such a condition in *Coryphodon*, in which the keels are but faintly indicated, and the two lateral grooves of which the primary keel forms the common median wall, are in the first stages of development. There is every reason to believe that this animal was plantigrade or subplantigrade in gait, and that the failure to develop the keels was due to the more equal distribution of the strain upon all the digits. This is true of the foot of the elephant in which we observe another structure which has certainly had much to do with the retardation of keel development viz: a very thick plantar pad. The possession of this pad not only tends to distribute the strain and equalize the pressure but at the same time limits the amount of flexion and extension of the phalanges. It is a fact worthy of especial note, and one which I will make use of later on, that in all these forms wherein the lateral grooves and keels are very little developed, the plantar border of the arcticular surface of the first phalanx is not at all notched. It is also to be noted that the feet are short and spreading.

With the assumption of the digitigrade position however, the plantar pad was reduced, the foot became more elongated, and the strain became more localized. In this position of the foot the weight of the body falls upon the phalanges, which are now bent at a considerable angle upon the metapodials, and an especial strain is produced by the flexor tendons where they pass over the distal ends of the metapodials. In a foot of this type therefore, do we find a considerable advance in the development of the median keel and lateral grooves of the metapodials? Those of the third digit are most advanced for the reason that the strain is more concentrated and localized

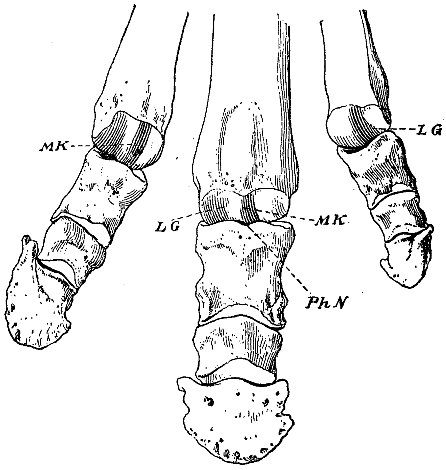

FIGURE 2.—Modern Tapir. Posterior or plantar surface of the hind foot.

at this point. In none of the metapodials however, do the lateral grooves and keel extend more than half-way around the articular ends, nor does the keel rise but little above the lateral boundaries of the grooves. This is well shown in such forms as the tapir, rhinoceros, *Hyracotherium* and nearly all the Eocene Perissodactyla. While the foot remained in the digitigrade position, the median keel of the metapodials made little or no impression upon the lower edge of the articular surface of the proximal phalanx, for the reason that the main flexure of the foot was between the first phalanges and the

metapodials, which would throw the keels so far back as to seldom come in contact with the proximal phalanx. In the middle toe or third digit, of the digitigrade foot however, the main flexure of this toe is momentarily transferred from the articulation between the metapodial and first phalanx to that between the second and third phalanges in the act of walking, and this straightening out of the first two phalanges, so as to bring them in a line with the long axis of the metapodial, has caused the keel to impinge upon the lower edge of the articular surface of the first phalanx which has become distinctly notched.

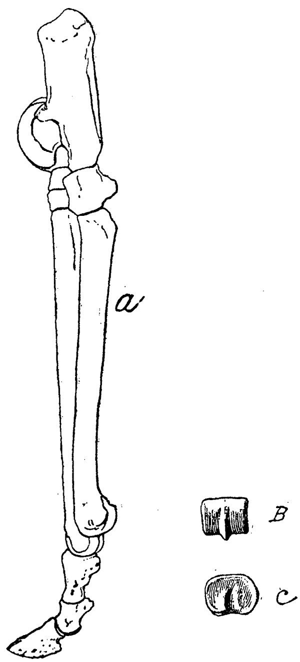

FIGURE 3.—*Mesohippus.* Outer view of the left hind foot. B, Distal surface of median metatarsal, C, Proximal surface of median first phalanx. (Collection Amer. Mus. Nat. Hist.)

It follows that in such forms as the tapir, rhinoceros, *Hyracotherium*, and in fact in all of the truly digitigrade Perissodactyla, the first phalanx of the median digit is always

slightly notched, while the first phalanges of the lateral digits are without the notch. This is an important fact, and in connection with what has just been said of *Coryphodon*, I think that it may be accepted as demonstrated, that the formation of this notch is due to the impact of the keel upon the lower border of the phalanx. Up to this stage therefore, we have the following conditions, viz: a comparatively low primary keel bounded upon either side by well marked lateral grooves whose outer borders are as much elevated as the keel. We also note that the grooves and keel extend but half-way around the end of the metapodial, and that the lower edge of the first phalanx in the middle toe is distinctly notched. This may be termed the digitigrade stage in the development of the keel.

In the next or unguligrade stage of this development, beginning with *Mesohippus*,[1] the foot changed from the digitigrade to the unguligrade position in which the main flexure of the foot was transferred to the articulation between the two last phalanges, and the two proximal phalanges came to occupy a position in line with the long axis of the metapodial. It is in this genus therefore, that we find the first distinctive evidence of an advance of the metapodial keel around the lower surface toward the dorsal aspect of the bone. While this advance or extension of the keel is slight, it is interesting to note that the notch in the first phalanx, which we see just beginning in the tapir, has now been transformed into a groove and extended nearly across the articular face of the bone. We are thus able to demonstrate that, in the further extension of the keel of the metapodial beyond that of the digitigrade stage, *the groove was formed in the phalanx first.* It is to be further noted that the keel has become prominent and that the lateral grooves of the metapodials are almost entirely obliterated, at least their outside walls have disappeared, leaving two nearly plain articular surfaces separated by a now prominent, or secondary median keel. Again, if the bones be placed in position,

[1]It is highly probable that the most incipient stages of this process are to be traced to forms somewhat older than this genus.

that is, if the first phalanx be articulated with the metapodial, it will been seen that when the phalanx is placed in a line with the metapodial or very nearly so, there is equal bearing upon all parts of the two articular surfaces of the bones ; but if the phalanx is flexed even to a slight extent, then the bearing falls largely upon the keel for the metapodial surface and the shallow groove for the phalangeal surface. When I say flexed I mean bent in the direction of the plantar side of the foot.

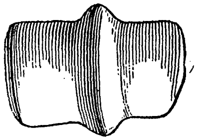

FIGURE 4.—Modern horse. Distal view of median metatarsal or cannon bone, showing complete keel.

How now can we apply these facts to the mechanical explanation of the further extension of the keel toward the dorsal side of the metapodials? When the foot assumed the unguligrade position permanently, we can understand, and have in fact already seen how the keel impinges upon and produces the notch in the phalanx. Any flexure of the phalanx upon the metapodial, under pressure would bring the keel to a more advanced position with reference to the phalangeal articulation, and would cause an extension of the notch in the phalanx so as to form a groove. That the phalanx is so flexed is evident to anyone who has ever studied carefully the movements of the foot of a horse in the act of pulling a heavy load up an inclined surface. Here the phalanx is seen to be greatly flexed when the foot strikes the ground and is therefore under great strain and pressure. I speak of it particularly in a horse pulling a load, because it is more noticeable in this case than in the unencumbered animal, but what is true of one is also true of the other. Now in an animal in which the keels and grooves were little or not at all advanced, such as was the case with the ancestor of the horse when he emerged from the digitigrade and assumed the unguligrade position of the foot, the flexure of the phalanx brought the keel forward and produced a groove in the phalanx. As the

phalanx went back to its more normal position, that is, in line with the long axis of the metapodial, there would then be a plane surface of bone lying immediately in front of the keel which would be opposed to a groove in the phalanx. An extension of the keel would necessarily follow as a result of moulding of this metapodial surface to fit the groove. Flexion, therefore, of the phalanx upon the metapodial under pressure, bringing the keel already formed to a more and more anterior position with reference to the articular surface of the phalanx, thus causing it to become grooved, and the subsequent moulding of the keel to fit this groove, I conceive to be the complete mechanical explanation of the production of this structure. The various stages in the forward extension of the keel is to be found in such series as *Hyracotherium*, *Epihippus*, *Mesohippus*, *Anchitherium*, *Hipparion* and *Equus*.

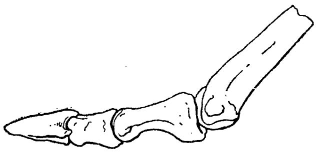

FIGURE 5.—Modern Tapir. Middle toe inside view, showing position of the phalanges upon the ground.

In the preceding discussion, only the possibility of the metapodial keels having been produced and extended forward by mechanical means, has been shown. I will now turn to the matter of the application of this reasoning to the somewhat broader question of the transmission of acquired characters, and see whether or not any argument can be adduced in support of the proposition that the development of these structures has been due *solely* to mechanical causes, and that they have in time been transmitted to succeeding generations. Upon this hypothesis it must be assumed that the changes took place first within the lifetime of the individual and that they finally came to be inherited. It must likewise be shown that wherever a groove or a keel has occurred, there must have been pressure, impact or strain, exerted at that particular point sufficient to accomplish the result. The only other pos-

sible explanation of these structures is upon the hypothesis of the accumulation of a number of spontaneous variations in this direction, entirely independently of any mechanical results acquired during the lifetime of the individual. According to this theory, all mechanical influence must of necessity, be rigidly excluded, for the reason that it is possible for it to have been exerted, or come into play only during the time that the foot was in use, and therefore, during the lifetime of the individual. If mechanical influence is admitted even to the slightest extent, then the whole proposition of the transmission of acquired characters is at once proven, and who can say how much is due to mechanics and how much to natural selection?

In the production of the completed keel and phalangeal groove, it must be shown by those who hold the theory of origin purely by natural selection that they are congenitally *correlated structures*, otherwise they must, according to the very nature of the case, have proven injurious to their possessor. In order for a keel to be useful it must be accompanied by a groove into which it is received. In other words it must be shown that any variation in the one *must have affected the other*. I shall now attempt to show that the keels and grooves are not congenitally correlated. It has been shown in the preceding pages, that the phalangeal notch which is the earliest and incipient stage of the phalangeal groove is *not* correlated with the keel. The evidence for this is to be seen in *Coryphodon*, *Elephas*, *Metamynodon*, *Titanotherium* and others in which the keel exists without any vestige of the phalangeal notch. Again, in the tapir and rhinoceros, the lateral metapodials are provided with distinct keels but the notch is absent. In the middle toe of many of the lower Perissodactyla, the keel is associated with the notch, but it was not until the foot assumed a position whereby it was possible for the keel to impinge upon the lower border of the phalanx that the notch appeared. It would indeed require a great stretch of the imagination to believe that the keel and notch were congenitally correlated structures in one toe and not in the others of

the same foot! In like manner it can be shown that neither the sesamoids, keels nor grooves of the metapodials are correlated structures, for we have seen that in the human thumb there are sesamoids present but no keels nor lateral grooves.

If upon the other hand we look at the problem from the standpoint here advocated of the mechanical explanation, or kinetogenesis, and we admit that the bone is plastic, then we are forced to conclude, it seems to me, that the lateral grooves and keels of the metapodials are the direct and unavoidable results of pressure exerted by the sesamoids. This is proven by the fact that wherever there are sesamoids present, and s t r o n g p r e s s u r e is exerted, there are developed lateral grooves and median keels, and that where the sesamoids are absent, or no pressure is exerted, there are no lateral grooves nor keels. As long as the foot remained in the digitigrade position the keel did not advance, and this is demonstrated by the fact that there is no animal of this gait that has a completed keel. Up to this point the lateral grooves and keel had a distinct function, viz: to serve as guides for the sesamoids, but when the change was made in the position of the foot to that of the unguligrade, the lateral grooves began to disappear and the keel, which we must regard in the light of a necessary accompaniment of these grooves, began to perform a new function. The excavation of the phalangeal notch, its extension into a groove, and the subsequent moulding of the metapodial surface into a secondary keel to fit the groove were just as much a mechanical necessity as was the original or primary formation of the lateral grooves and keel. The proof of this is to be found in the fact that in the further extension of the keel beyond the digitigrade stage, the phalangeal groove led the way. In the mechanical explanation therefore, we have every condition satisfied, while upon the theory of natural selection of favorable variations the explanation is vague, unsatisfactory and not in accord with the facts.

American Museum of Natural History, March 29th, 1893.